EYES OF DEEP SEA CRUSTACEANS

I. ACANTHEPHYRIDÆ

J. H. WELSH AND F. A. CHACE, JR.

(From the Woods Hole Oceanographic Institution¹ and the Biological Laboratories, Harvard University)

The depths of the ocean impose upon the animals which live there a very different set of environmental conditions from those found at the surface. Absence of sunlight, low temperature, high pressure and viscosity, and a somewhat different chemical composition of the sea water necessitate morphological and physiological modification in the organisms which inhabit deep water. Some of these modifications are well known. For example, if we select the more obvious features which are associated with low light intensity, or even complete absence of sunlight, we must include the presence of photophores, peculiar pigmentation of the body, and adaptation of the eyes for vision at a very low intensity of illumination. The photophores and eyes of certain groups of deepsea crustaceans and fishes have been studied in some detail in the past and are reasonably familiar to biologists. One of the first and best known studies in which the structure of the eve was related to depth was that of Beddard (1884) on the isopod genus Serolis. A similar study was made later (Beddard, 1890) on the genus Arcturus. Smith (1886) and Henderson (1888) had already noted the tendency toward degeneration in the eves of deep-water crustaceans, but neither had made a detailed study of these eyes. Chun's (1896) study of the very unusual eyes of deep-water euphausiïds was made from collections of the "Challenger" as were Beddard's.

From the collections of the "Valdivia," Doflein (1904) obtained material for a valuable study of the eyes of deep-sea crabs. Dohrn (1908) described the eyes of a few other crustaceans taken by the "Valdivia." More recently Hanström (1932–33) has had an opportunity to study the eyes of deep-water crustaceans.

The problem which confronted these workers, and many others who have made more casual observations, was to explain why some forms found in deep water have well-developed and apparently functional eyes while others are completely blind or have very degenerate eyes. This still remains the most interesting problem in connection with a con-

¹ Contribution No. 126.

sideration of the effect of depth and hence of diminishing light on the eye. There are many more problems which the older investigators would have doubtless solved if they had had more material from known depths, living material, and a more constant supply.

The regular operation of the research vessel "Atlantis" of the Woods Hole Oceanographic Institution has made it possible to study further the animals of the deep sea and has led to the planning of a program in which the first step has been to investigate more fully the modifications with depth in the eyes of certain of the crustaceans. What happens to the size of the eye, the number of ommatidia, the amounts of reflecting and screening pigments, pigment migration, and the structure of the rhabdomes with increasing depth? What is the relation between the development of the eye and the presence or absence of photophores? Such questions, dealt with in an introductory manner, using for material certain representative deep-sea acanthephyrids or prawns, are those we wish to discuss in the present paper. Final conclusions must await the study of many more types of crustaceans from known depths, but certain tendencies are noticeable in the work thus far carried out.

The authors are indebted to several members of the Woods Hole Oceanographic Institution, particularly to Dr. H. B. Bigelow, and to Mr. B. B. Leavitt from whose collections, made in a study of the vertical distribution of deep-water plankton, some of the material for the present study was obtained. The expense of preparing the eyes histologically has been cared for in part by a grant from the Milton Fund of Harvard University.

METHODS

The first problem in understanding the effect of the physical environment on deep-sea animals is to obtain a series of a given species from known levels, sufficiently large so that it is possible to determine the average level at which such a species lives. The use of open nets is unsatisfactory as animals are caught at all levels, and only after a large number of hauls at a given station can an idea of the vertical distribution of a species be determined. Nets which may be sent down to the desired level closed, then opened and towed at that level, and finally closed before being brought to the surface are almost a necessity. To operate two to five such nets, particularly when towing at depths of one to two miles, presents mechanical problems which have been quite adequately solved. The closing net used in deep-water tows from "Atlantis" previous to 1936 is described in a paper by Leavitt (1935). The type of net used during the 1936 cruise was modified somewhat and was found to be well adapted for collecting material alive or in good condition. It will be described in a later paper.

The locations of stations from which material was obtained in 1933 and 1934 are given by Leavitt (1935). During July, 1935, two stations were made in the Sargasso Sea: Station No. 2462 (42° 29' N. and 70° 21' W.) and No. 2463 (42° 27' N. and 70° 14' W.). During late August, 1935, one station was made on the inshore side of the Gulf Stream: No. 2475 (38° 25' N. and 71° 04' W.). In September, 1936, collections were made at Station 2666 (39° N. and 70° W.) and at Station 2667 (35° 40' N. and 69° 36' W.).

Obtaining deep-water animals living and in good condition is a second difficulty. Where there may be a warm surface layer, as on the slope side of the Gulf Stream, the animals coming from deeper layers are subjected to a considerable increase in temperature which, it is believed, is much more damaging than the reduction in pressure. The following temperatures were found in early September, 1936.

| Station 2666 Slope side of Gulf Stream | Station 2667 Sargasso Sea |
|---|------------------------------|
| slope side of Guil Stream | Salgasso Sca |
| Depth Temp. °C. | Temp. °C. |
| Surface 21.0° | 26.2° |
| 200 m 9.7° | 18.3° |
| 400 m 5.4° | 17.8° |
| 800 m 4.5° | 14.9° |
| 1000 m 4.2° | 11.7° |
| 2000 m 3.6° | 4.3° |

It may be seen that while there was a difference of 5.2° C. at the surface, at 400 m. there was a difference of 12.4° C. Many more of the larger crustaceans were living when they arrived at the surface at Station 2667 than at Station 2666.

During the two trips in 1935 an opportunity was had for the first time to study living forms. Among the acanthephyrids only one species, *Systellaspis debilis*, was obtained alive in any considerable numbers. The only requirement for keeping this form living was found to be a low temperature. At 10° C, they survived for three days, at the end of which time they were killed; therefore, at that time it was not known how much longer they would have lived. During the 1936 cruise a cooling system was on board which made it possible to maintain tanks of sea water at 5° C. Many more forms were taken alive and several species of crustaceans were kept living for the duration of the cruise. Apparently it is possible to maintain many deep-water forms alive if they are kept at a temperature relatively the same as that where they normally live.

The material used for histological study was fixed in Bouin's immediately on removal from the nets or, in cases where it was desired to observe pigment migration, was kept illuminated for a period of time before fixing. It was found quite necessary to cut through the carapace in order to obtain sufficiently rapid penetration of the fixative. The paraffin method was used in sectioning the eyes. In estimating relative amounts of pigment it was found desirable to leave some sections of each eye unstained. Ehrlich's hæmatoxylin and a counter of eosin were employed for staining those sections which were used in studying the general structure.

MATERIAL

Although certain species of the Acanthephyridæ are so numerous that the possibilities of fishing for these prawns on a commercial scale have been suggested, it was as late as 1881 before more than two species of the family were known. Today, due to the many deep-sea expeditions in the past fifty years, the family is represented by six genera and forty-five species. The acanthephyrids normally inhabit the deeper parts of the sea where the penetration of sunlight is practically immeasurable—the so-called "red prawn-black fish" region.

Like a number of other deep-sea animals which have been known to science for only a short time, the acanthephyrids are a comparatively primitive group. The biramous form of the legs, one of the most distinctive characters of the family, ranks them among the most primitive members of the decapod Crustacea. Their color, with but a few exceptions, is a uniform deep crimson red. In other respects the species may differ so noticeably from each other that a cursory examination would scarcely lead to their inclusion in a single family. The integument varies from a hard, polished, armor-like shell to a membranous skin which is displaced or torn from the slightest handling; the rostrum or "head-spine" is typically long and slender, but in many species it is almost entirely lacking; the legs may be short and comparatively stout, or long, slender and fragile, or they may be modified, as in Ephyrina, into broad, lamellate appendages; and the eggs are either so small that many hundreds may be attached to a single female, or so large that twenty-five would be a burden to even the larger species. It will soon be seen that this diversity of form is likewise illustrated by the eves of these prawns. Since most of the species are strictly bathypelagic organisms, they probably obtain their food from the detritus that is constantly raining down from the swarms of minute plants and animals at the surface of the sea. They are peculiarly adapted to strain this food from their surroundings; the thoracic legs are all provided with numerous long hairs and spines which apparently form a very efficient, sieve-like basket when the legs are held curved beneath the body. In the genus *Ephyrina* the legs are strikingly wide and flat so that, when held in position, they perform their function in much the same way as the baleen of the whale-bone whales. This modification of the legs for food-gathering is of particular interest when one realizes that the thoracic limbs of most shrimp-like Crustacea are used primarily for walking on the sea-bottom and play no direct part in the swimming movements of the animal. Since many of the acanthephyrids probably spend their entire lives far above the sea-floor, the thoracic legs would be only a hindrance to the progress of the prawn through the water if they were not modified to perform a function entirely apart from that for which they were originally designed.

There are, of course, few barriers to the dispersion of bathypelagic organisms which inhabit a world-wide zone of comparative uniformity of temperature and salinity. Many of the Acanthephyridæ, as in most families containing a like number of forms, are known from a very few specimens and little can be concluded about the distribution of those forms at present; but of the commoner ones, some are practically cosmopolitan, some seem to have a discontinuous range, while still others are confined to a reasonably small area. The Indo-Malayan region has the largest representation of these species, if our present records are reliable, with the North Atlantic second in importance. It is a curious fact that there are at least three reasonably common species in the Indo-Malayan region which so far have not been encountered elsewhere, but all three of these species show a very close relationship to three other forms which have been found almost everywhere except in the Indian Ocean. Much more data must be accumulated before the factors responsible for the specific isolation of bathypelagic organisms are known.

As regards the vertical distribution of the group the available data are likewise incomplete. However, of the forty-five species, thirty have been taken with mid-water nets and must be bathypelagic for at least part of the time. Further investigation will undoubtedly reveal that at least some of the remaining fifteen species seldom go down to the sea-floor. On the other hand, three stout-legged, heavy-bodied forms which have always been taken with the dredge or trawl can safely be termed benthonic animals. Investigations undertaken in the past few years by Mr. Leavitt on "Atlantis" have yielded invaluable information regarding the actual depths at which we may expect to find acanthephyrids in the North Atlantic. The accompanying tables (Tables I, II, and III) give the depths at which three of the most common Atlantic species have been taken with closing nets. Incomplete as these records are, it is quite evident that *Hymenodora glacialis* normally frequents a deeper zone than either of the other species, a fact which agrees with earlier data. *Acanthe*-

| Depth in meters | "Atlantis" Station | Number of specimens | Total specimens |
|-----------------|----------------------|---------------------|-----------------|
| 300 | 1737 | 1 | 1 |
| 400 | 2263 | 10 | 10 |
| 800 | 2263 2462 2463 | 65 7 2 | 74 |
| 920 | 2216 | 10 | 10 |
| 1000 | 2260 2263 | 1 2 | 3 |
| 1400 | 2263 | 1 | 1 |
| 1600 | 2263 | - 1 | 1 |
| 1800 | 2216 | 2 | 2 |
| 2200 | 2263 | 1 | 1 |
| 2600 | 2260 | 2 | 2 |

TABLE I

Depths at which specimens of Acanthephyra purpurea have been taken with closing nets by the "Atlantis."

phyra purpurca has been taken in open nets from the surface, where one specimen was collected with a dip-net down to 2800 meters, but the majority have been found between 400 and 1000 meters. *H. glacialis* has been found on two occasions at the surface in the Arctic, and some numbers of that species have been found in the stomachs of arctic seabirds. The shallowest trustworthy record for the species taken with midwater nets, however, is one in which ten specimens were taken in 750 meters, and by far the largest number of specimens have come from

EYES OF DEEP SEA CRUSTACEANS

TABLE II

Depths at which specimens of Systellaspis debilis have been taken with closing nets by the "Atlantis."

| Depth in meters | "Atlantis" Station | Number of specimens | Total specimens |
|-----------------|--------------------|---------------------|-----------------|
| 400 | 2263 | 15 | 15 |
| 600 | 2260 | 1 | 1 |
| 800 | 2462 | 9 | 9 |
| 1800 | 2263 | 1 | 1 |

depths greater than 1000 meters. This species has also been taken with a closing net by the "Valdivia" Expedition in over 4200 meters in the South Pacific. *Systellaspis debilis* apparently frequents slightly shallower depths than the other two species, regardless of the fact that it is the only one of the three which has not been found at the surface. It has been collected with open nets between 32 and 2000 meters and appears to be most abundant between 150 and 500 meters.

At present little is known of the daily vertical migration of these

TABLE III

Depths at which specimens of Hymenodora glacialis have been taken with closing nets by the "Atlantis."

| Depth in meters | "Atlantis" Station | Number of specimens | Total specimens |
|--------------------|--------------------|---------------------|-----------------|
| 1000 | 2463 | 2 | 2 |
| 1200 | 2462 | 3 | 3 |
| 1400 | 2263 | 4 | 4 |
| 1600 | 2263 2475 | 2 3 | 5 |
| 2000 | 1737 | 3 | 3 |
| 2200 | 2263 | 1 | 1 |
| 2600 | 2260 | 2 | 2 |
| 2800 to 3200 | 1739 | 1 | 1 |

species. The results of past expeditions seem to indicate a very slight movement toward the surface at night in *.4. purpurea* and *S. debilis* but absolutely none in *H. glacialis* (Murray and Hjort).

An examination of the external features of the eyes of these and other acanthephyrids offers a partial explanation of the above findings. The form of the eyes, although extremely diversified in the group as



(Figures 1-6 are dorsal views of the right eye and eyestalk)

- Fig. 1. Acanthephyra purpurea, \times 5.
- Fig. 2. Ephyrina benedicti, male, $\times 4$.
- FIG. 3. Notostomus longirostris, small female, \times 5.
- FIG. 4. Systellaspis debilis, \times 7.5.
- FIG. 5. Oplophorus grimaldii, male, \times 7.5.
- FIG. 6. Hymenodora glacialis, male, \times 7.5.

a whole, remains fairly constant within the separate genera. The eyes of the species of *Alcanthephyra* (Fig. 1) are of normal size, generally well pigmented with a dark brown pigment and, as in the other genera, the dorsal surface of the eyestalk is provided with an incomplete, deeply pigmented ocellus or accessory cornea, whose function is unknown. In some species the ocellus is complete and entirely distinct from the true cornea, while in others it may be partially fused with the cornea or even entirely absent. The eyes of Ephyrina (Fig. 2) and Notostomus (Fig. 3) while similar in size and shape to those of Acanthephyra have a jet-black pigment which remains for many years even in alcohol. In Systellaspis (Fig. 4) the cornea is considerably larger in proportion to the stalk than in the foregoing genera. The extreme size is attained in the species of Oplophorus (Fig. 5) in which the eye may be actually broader than long, and the cornea is generally set diagonally on the end of the stalk. It is worthy of note that these large-eyed species of Systellaspis and Oplophorus possibly all possess photophores. The other extreme is found in the eyes of the two species of Hymenodora (Fig. 6). In these forms the corneal portion is reduced to a size which is considerably smaller in diameter than the eyestalk. On recalling the records concerning the vertical distribution, it will be seen that those species which have the largest eyes apparently frequent the shallower layers of water, while those with vestigial eyes, like Hymenodora, may be termed truly abyssal forms.

The accompanying graph (Fig. 7), despite inaccuracies that can scarcely be eliminated in measuring tissues so subject to alteration after preservation, clearly indicates that the eyes increase in diameter in proportion to the length of the carapace. It is also quite obvious that the degenerate eyes of *Hymenodora* increase in size very little with the growth of the animal. Perhaps the most striking fact brought out by these measurements, however, is that the eyes of *Oplophorus grimaldii* and *Systellaspis debilis*, two forms bearing photophores, are larger in relation to body size than are the eyes of those forms lacking huminescent organs.

Comparative Structure of the Eyes

Fortunately the three most abundant species of acanthephyrids in the North Atlantic and therefore those whose vertical distribution is best known, represent three possible trends in the development of the eye. *Acanthephyra purpurca* is found in greatest numbers within the photic zone, and as it shows a diurnal migration this species must be influenced by the penetrating daylight, although of extremely low intensity. Even in the Sargasso Sea, where the water is very clear, the intensity of blue light at noonday may be reduced to 0.5 per cent of the light at the surface, at a depth of 180 meters (Clarke, 1933). The penetration of other components of daylight into Atlantic waters may be found in a paper by Oster and Clarke (1935). *A. purpurca* is

7

found far below 180 meters during the day; hence it must be subjected to a very low intensity of illumination.

Systellaspis debilis has much the same vertical distribution as A. purpurea, but this form possesses numerous photophores, and, as has already been pointed out, there is an apparent correlation between the size of the eye and the presence or absence of photophores, for species



FIG. 7. The diameters of the eyes of four series of acanthephyrids are here shown plotted against carapace length. *Oplophorus* and *Systellaspis* have photophores.

of *Systellaspis* and *Oplophorus* have larger eyes in proportion to body size than the other genera of acanthephyrids which lack photophores.

The ability to emit clouds of luminous material is possessed by certain of the deep-sea prawns, as has been mentioned by Alcock (1902) and by Beebe, who observed this phenomenon frequently in his bathysphere descents. So little is known of this interesting method of illuminating the surroundings that it is not possible to hazard a guess as to its effect on the development of the eye. The third species, *Hymenodora glacialis*, inhabits a region well below the photic zone and does not possess photophores and it will be shown that the eyes of this species are very degenerate structurally.

It will not be necessary to describe the general plan of the eve of acanthephyrids for it is basically like that of other decapod crustaceans, and such eyes have been described by Parker (1891), Patten (1887), Trojan (1913), to mention only a few of the earlier investigations of the histology of decapod eyes. From the standpoint of vision and visual acuity the most important features to be considered in any compound eve are the following: (a) number of ommatidia, (b) development of the rhabdomes (the receptor units), (c) amounts, distribution. and movements of screening and reflecting pigments. To these should be added the photosensitive material contained in the rhabdomes. So little is known of the nature of this material that it cannot be discussed at the present time. The average number of ommatidia in a longitudinal section of an eye may be taken as a measure of the total number of ommatidia and thereby the task of counting all the elements is avoided. In all counts the eyes of large, mature individuals were selected, although not the largest obtainable. In eyes of mature A. purpurea (Fig. 10) averaging 2.5 mm, in diameter the average number of ommatidia in a section was found to be 145. Eyes of mature S. debilis averaging 1.9 mm. in diameter had an average of 81 ommatidia. Eyes of H. glacialis averaging 0.6 mm, in diameter had an average of 22 ommatidia. The number of ommatidia, hence the number of rhabdomes. determines in part the visual acuity of an arthropod; therefore the variation in number in these three forms must be significant.

The rhabdomes, whence the fibers of the optic nerve arise, are in a sense the most important structures found in the compound eye. A single rhabdome is formed of parts of the seven functional retinular cells found in each ommatidium, and a longitudinal section presents a peculiar striated appearance. In none of the acanthephyrids which have been studied do the rhabdomes have the well-defined outlines seen in the majority of decapods, including certain deep-water forms. Of the three species being especially considered they are perhaps most definite in *S. debilis*, and may be seen in sections of the eyes of lightadapted specimens (Fig. 15) where they are outlined by the proximal pigment. In *A. purpurca* they are difficult to distinguish (Fig. 9). In all forms taken from the nets during either day or night they were never surrounded by pigment. This means that light entering a given ommatidium could reach the rhabdomes of neighboring ommatidia (Exner, 1891).



FIG. 8. Dorsal view of the head of A. purpurca, $\times 2$.

FIG. 9. Photomicrograph of a section of the eye of a young A. purpurca, \times 40. FIG. 10. Photomicrograph of an unstained section of the eye of a mature A. purpurca, \times 40.

Fig. 11. Reflecting pigment of the eye of a young A. purpurea as seen by reflected light, \times 35.

FIG. 12. Reflecting pigment of a mature A. purpurea, \times 35.

In *H. glacialis* the rhabdomes are entirely lacking. The nuclei of the retinular cells remain, and a few nerve fibers leave their vicinity (Fig. 13). At best the eye of this form can be used only as a light receptor. While not as degenerate as the eyes of certain blind crayfish (Parker, 1890) there is certainly not the necessary visual apparatus for image reception.

Eve Pigments

Unpublished results obtained by one of us from keeping certain decapods in constant darkness for a period of months indicate that there may be a gradual reduction in the amount of screening pigment in the eye. This is perhaps to be expected from the work of Odiorne (1933) on the effects of black and white backgrounds on the body pigments of certain fishes. Is there any correlation in the acanthephyrids under consideration between depth and the amounts of screening and reflecting pigment? In practically all decapod crustaceans from shallow water there are two sets of screening pigments. The so-called distal or irispigment is found around the cones, and in many forms such as *Palamonetes* (Welsh, 1930) it migrates in and out under the influence of hormonal action (Kleinholz, 1936), forming the pseudopupil which helps to regulate the amount of light reaching the rhabdomes. In certain shallow-water prawns which are distinctly nocturnal in their habits such as *Penæopsis goodei* (Welsh, 1935) and species of Brachycarpus and Rhynchocinetes, the eyes of which have not been described, the distal pigment forms a collar around the outer ends of the cones and remains in that position in light and dark-adapted eyes. In S. debilis the distal pigment is present in an amount comparable to that found in nocturnal surface forms while it is slightly less dense in A. purpurea and completely lacking in H. glacialis. In specimens of S. debilis, light-adapted for three hours, there was no measurable migration of the distal pigment. In specimens of both A. purpurea and S. debilis, fixed directly from the nets either during the day or night, the distal pigment was always in the extreme outer position.

The second set of screening pigment, the proximal pigment, is found in the retinular cells. In dark-adapted eyes of decapods in general, the main mass is found below the basement membrane, while in the light it moves peripherally to surround the rhabdomes and migrates between the plates. In this position it absorbs a large part of the light which reaches the rhabdomes before it has penetrated to any considerable depth. In all specimens of *A. purpurea* and *S. debilis* taken from the nets during the day or night the proximal pigment never surrounded the rhabdomes and the major portion was in the position characteristic of extreme dark adaptation. In adults of these two species this pigment is present in about equal amounts, but is much less dense than in nocturnal forms found in surface waters. In young of A, purpurca, however, the proximal pigment is very heavy in the lateral portion of the eye (Fig. 9). In *H. glacialis* the proximal pigment is entirely lacking as is the distal pigment.

If we assume that the diurnal vertical migrations of A. purpurea and S. debilis keep these forms in a region of very low but constant light intensity, it would be interesting to know whether the proximal pigment still retains the ability to migrate around the rhabdomes when these forms are subjected to illuminations of high intensity. It was possible to test this point with S. debilis and A. purpurea. Figure 16 is a photomicrograph of a section of the retina of a specimen of S. debilis which had been kept in darkness for three days. Figure 15 is of a similar region of the retina of a specimen kept in diffuse daylight for one hour. During this time the pigment had migrated for some distance peripherally and had surrounded the proximal two-thirds of the rhabdomes. This indicates that the ability of the proximal pigment to migrate still persists even though it may never do so normally in the lifetime of the organism. The proximal pigment of A. purpurea is also capable of movement although after prolonged light-adaptation it seldom migrates far into the retinular cells.

The reflecting pigment of decapod eyes is a layer of amorphous guanin which is concentrated around the bases of the retinular cells and acts as a mirror to reflect light back into the rhabdomes (Welsh, 1932). A reflecting or tapetal layer is found in most animals which are active during the night or which live in a region of low light intensity; therefore it is not surprising that this pigment layer is welldeveloped in the eyes of deep-water decapods.

EXPLANATION OF FIGS. 13-18

FIG. 13. Section of the eye of H. glacialis photographed with transmitted light, $\times 60$.

FIG. 14. Section of the eye of *II. glacialis* photographed by means of reflected light, \times 60.

FIG. 15. Region of the retinular cells and rhabdomes of a light-adapted eye of S. debilis, \times 175.

FIG. 16. Region of the retinular cells and rhabdomes of a dark-adapted eye of S. debilis, \times 175.

Fig. 17. Section of a portion of the eye and the papilla of O. grimaldii photographed with transmitted light, \times 50.

FIG. 18. The same photographed with reflected light, \times 50.

EYES OF DEEP SEA CRUSTACEANS





J. H. WELSH AND F. A. CHACE, JR.

The eyes of A, purpurea and S, debilis have this reflecting layer in addition to the usual screening pigments (Figs. 11 and 12) while H, glacialis has only reflecting pigment (Fig. 14). The quantity of reflecting pigment in H, glacialis is greater in proportion to the size of the eye than in the other two forms under consideration. It is worth noting that in a series of five species of Scrgestes which have been studied in a preliminary way there is a rather striking correlation between the amount of reflecting pigment and the depth at which the several forms were taken.

Discussion

The gradual modification of an organ such as the eve as a result of environmental changes, or changes in habit, is one of the fascinating aspects of evolution. A comparison of the eyes of forms which are active at night with those which are active during the day reveals structural and functional adaptations which are among the best examples of the manner in which living material may be modified by external conditions. The degeneration of the eve of cave cravfishes (Packard, 1888; Parker, 1890) is a striking illustration of the disappearance of a useless organ. In the sea we have a gradual reduction in the amount of sunlight which penetrates into the water until a depth is reached, which varies with the locality, at which there is a complete absence of sunlight. The animals of the deep sea have without much question evolved from shallow water forms. Their eves have become modified depending on the depth to which they have migrated. In regions of low light intensity they are, in general, so changed by an increase in size, loss of screening pigment, and in other ways that they are doubtless quite effective organs of sight. Below the level to which light penetrates some are degenerate and some are completely lacking. On the other hand, some are large and, structurally at least, well adapted for vision or for light reception. This fact still remains as one of the most baffling problems associated with the biology of deep-sea animals. Can there be enough light produced by luminescence to account for the well-developed eves of some abyssal forms, particularly those living on bottom? This is the question with which most discussions of the eyes of deep-sea animals have ended. It is our hope that if the opportunity remains to continue these studies this question may be satisfactorily answered.

SUMMARY

1. Three species of acanthephyrids have been taken in closing nets in the region of the Sargasso Sea and in slope water near the Gulf Stream in numbers sufficient so that their vertical distribution is quite accurately known.

Acanthephyra purpurea and Systellaspis debilis are found mostly within the photic zone. Hymenodora glacialis inhabits a region below that to which sunlight penetrates.

2. The eyes of *A. purpurea* and *S. debilis* are quite similar structurally to the eyes of shallow-water prawns, except that there is less screening pigment.

3. Species of *Systellaspis* and *Oplophorus* possess photophores and the eyes of these forms are larger in proportion to body size than the eyes of those acanthephyrids which lack photophores.

4. The eyes of *H. glacialis* are quite degenerate. The rhabdomes, and both distal and proximal pigments are lacking. The reflecting pigment layer is well developed.

5. Characteristic movements of the proximal pigment of *S. debilis* and *A. purpurea* occur as the result of light adaptation.

LITERATURE CITED

ALCOCK, A., 1902. A Naturalist in Indian Seas. John Murray, London.

- BEDDARD, F. E., 1884. Report on the Isopoda Collected by H. M. S. Challenger. Part I. The Genus Serolis. Zoöl. Chall. Exp., 11: Part 33.
- BEDDARD, F. E., 1890. On the minute structure of the eye in some shallow-water and deep-sea species of the isopod genus Arcturus. *Proc. Zoöl. Soc. London*, **26**: 365.
- CHACE, F. A., JR., 1936. Revision of the bathypelagic prawns of the family Acanthephyridæ, with notes on a new family, Gomphonotidæ. Jour. Wash. Acad. Sci., 26: 24.
- CHUN, C., 1896. Biologische Studien über pelagische Organismen. VI. Leuchtorgane und Facettenaugen. Bibliotheca Zoologica, 7: 191.

CLARKE, G. L., 1933. Observations on the penetration of daylight into mid-Atlantic and coastal waters. *Biol. Bull.*, **65**: 317.

- DOFLEIN, F., 1904. Brachyura. Wissenschaftliche ergebnisse der Deutschen Tiefsce-Expedition., 6: 1.
- DOHRN, R., 1908. Ueber die Augen einiger Tiefseemacruren. Inaugural Diss., Marburg.
- EXNER, S., 1891. Die Physiologie der facettirten Augen von Krebsen und Insecten. Leipzig und Wien.
- HANSTRÖM, B., 1932. Neue Untersuchungen über Sinnesorgane und Nervensystem der Crustaceen. II. Zoöl. Jahrb., Anat., 56: 387.

HENDERSON, J. R., 1888. Report on the Anomura Collected by H. M. S. Challenger. Zoöl. Chall. Rcp., 27: Part 49.

- KLEINHOLZ, L. H., 1936. Crustacean eye-stalk hormone and retinal pigment migration. *Biol. Bull.*, **70**: 159.
- LEAVITT, B. B., 1935. A quantitative study of the vertical distribution of the larger zoöplankton in deep water. *Biol. Bull.*, 68: 115.
- MURRAY, J., AND J. HJORT, 1912. The Depths of the Ocean. Macmillan and Co., Ltd., London.
- ODIORNE, J. M., 1933. Degeneration of melanophores in Fundulus. Proc. Nat. Acad. Sci., 19: 329.

- OSTER, R. H., AND G. L. CLARKE, 1935. The penetration of red, green and violet components of daylight into Atlantic waters. Jour. Opt. Soc. Am., 25: 84.
- PACKARD, A. S., 1888. The cave fauna of North America, with remarks on the anatomy of the brain and origin of the blind species. *Mem. Nat. Acad. Sci.*, **4**: 3.
- PARKER, G. H., 1890. The eyes in blind crayfishes. Bull. Mus. Comp. Zoöl., 20: 153.
- PARKER, G. H., 1891. The compound eyes in crustaceans. Bull. Mus. Comp. Zoöl., 21: 45.
- PATTEN, W., 1887. The eyes of molluses and arthropods. *Jour. Morph.*, 1: 67. SMITH, S. I., 1880. The abyssal decapod crustacea of the "Albatross" dredgings
- SMITH, S. I., 1886. The abyssal decapod crustacea of the "Albatross" dredgings in the North Atlantic, 17: 187.
- TROJAN, E., 1913. Das Auge von Palaemon squilla. Denkschr. kais. Akad. Wiss., Wien, 88: 291.
- WELSH, J. H., 1930. The mechanics of migration of the distal pigment cells in the cycs of Palæmonetes. *Jour. Exper. Zoöl.*, **56**: 459.
- WELSH, J. H., 1932. The nature and movement of the reflecting pigment in the eyes of crustaceans. Jour. Exper. Zoöl., 62: 173.
- WELSH, J. H., 1935. Further evidence of a diurnal rhythm in the movement of the pigment cells in the eyes of crustaceans. *Biol. Bull.*, 68: 247.